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Inferring extinction risks from sighting records

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HIGHLIGHTS

- We infer extinction using certain and uncertain sightings, together with expert estimates for observing the species.
- We examine two different approaches to handle uncertainty in the expert estimates.
- The model is more general than existing models, hence reduces to an existing model for certain, limiting cases.
- The inference for species extinction depends on how one treats uncertainty in the expert estimates, and the inclusion of uncertain sightings.

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ABSTRACT

Estimating the probability that a species is extinct based on historical sighting records is important when deciding how much effort and money to invest in conservation policies. The framework we offer is more general than others in the literature to date. Our formulation allows for definite and uncertain observations, and thus better accommodates the realities of sighting record quality. Typically, the probability of observing a species given it is extant/extinct is challenging to define, especially when the possibility of a false observation is included. As such, we assume that observation probabilities derive from a representative probability density function. We incorporate this randomness in two different ways ("quenched" versus "annealed") using a framework that is equivalent to a Bayes formulation. The two methods can lead to significantly different estimates for extinction. In the case of definite sightings only, we provide an explicit deterministic calculation (in which observation probabilities are point estimates). Furthermore, our formulation replicates previous work in certain limiting cases. In the case of uncertain sightings, we allow for the possibility of several independent observational types (specimen, photographs, etc.). The method is applied to the Caribbean monk seal, *Monachus tropicalis* (which has only definite sightings), and synthetic data, with uncertain sightings.

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1. Introduction

Extinction is the currency of conservation biology. Knowing the probability that a species is extinct allows informed decisions to be made about investing time and money into its preservation, and carrying out surveys. On a broad scale, extinction rates are used to measure biodiversity conservation effectiveness (May et al., 1995; Commonwealth of Australia, 1996; Flannery and Schouten, 2001; IUCN, 2002). Incorrectly classifying a species as extinct or extant can lead to failure to conserve a threatened species, wasted conservation effort directed toward a species that is mistakenly thought to persist, or erosion of public confidence when a species reappears after being classified as extinct (the Lazarus effect Keith and Burgman, 2004). Extinctions of particular species are rarely observed directly and, in many cases, can only be inferred from sighting or collection records (Solow and Roberts, 2003). Solow (1993), Burgman et al. (1995), McCarthy (1997) and Rout et al. (2009) developed and applied mathematical models to indicate whether a species is extinct based on a list of time intervals (usually years) in which the species was sighted. More recently, Solow et al. (2011) and Lee et al. (2013) developed models which account for uncertain sightings (i.e., where there was uncertainty or debate about the validity of the sighting) hence avoiding problems about whether or not to include this data. Lee et al. (2013) provide comparisons where uncertain sightings are excluded from the sighting data, and where they are included, but treated as uncertain sightings (i.e. "false positives" are possible). Their findings confirm the intuition that formally accounting for uncertain

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sightings provides different probabilities for extinction than simply including/excluding them as definite sightings. In keeping with this new generation of extinction models, we also formally account for uncertain sightings.

Consider the ecological problem as a system which can be in one of the two states, extinct or extant. The complete system is the number of years (or other time period) since the species was first discovered. The true state of the system is whether the species was extant/extinct in each year, where clearly the species is extinct every year after extinction first occurred. Similar to Solow (1993), Solow et al. (2011) and Rout et al. (2009), we infer the state of a species by calculating the probability that a species is extant given the sighting data. The problem has several random variables, including the prior probability that a species is extinct/extant, and the probabilities of an observation given the species is extinct/extant. The latter carries more ambiguity, especially when false sightings are considered. Hence, Solow et al. (2011) and Lee et al. (2013) focus on randomness in the rate of sightings. Therefore, we consider the probability of an observation (given extinct/extant) as drawn from a probability density function (pdf), and use a point estimate prior. The ensuing analysis makes use of a formulation that is equivalent to a Bayesian approach, with some parallels to Solow (1993), Solow et al. (2011), and Lee et al. (2013). However, it is a far more general methodology.

Unlike previous work, we use two different methods to account for uncertainty in the probabilities of an observation given the species is extant/extinct. We show that one of our methods reduces to the work of Solow (1993) in certain limiting cases. When the pdf's for probability of an observation (given extinct/extant) reduce to a point estimate, the methods reduce to a deterministic inference for extinction.

Throughout this paper, we refer to one method as the annealed approach, and the other as the quenched approach. This terminology arises from the similarities between our ecological problem, and the statistical mechanics of spin glass in physics (Brout, 1959; Thompson, 1983; Wang et al., 1990; Binder, 2001), which has also been applied in a range of problems in biology (Hopfield, 1982; Amit et al., 1985; Mezard et al., 1987).

More detail about the differences between the approaches is given in Section 2, with a trivial example to illustrate the implementation of the quenched and annealed approaches. In Section 3 we consider the case of definite sightings only, which relates to the well-recognised work of Solow (1993). We use the Caribbean monk seal as an example with definite sightings only. Lastly, in Section 4 the concept of multiple sightings records, each with varying probabilities of the sightings being true (as in Lee et al., 2013), is worked into the model. The model is demonstrated on a sample data set.

2. A general theoretical framework

2.1. Formulation

We represent a sighting record over a period of T time steps, such as years, by the vector

$$\boldsymbol{s} = (s_1, s_2, \ldots, s_T),$$

where s_i denotes the sighting state in year $i = 1, 2, \ldots, T$ which could include one or a combination of specimens, photographs, sounds, observations, reports, surveys, etc. The state of the species over the T year period can also be represented by a vector

$$\boldsymbol{\sigma} = (\sigma_1, \sigma_2, \ldots, \sigma_T),$$

but with the simplifying feature that the σ_i have only two possible states: extant x and extinct e in years $i = 1, 2, \ldots, T$. Thus if the species is extant in year i ($\sigma_i = x$) it must be extant in all previous years. Similarly, if the species is extinct in year i ($\sigma_i = e$), it must be extinct in all subsequent years. Let T_N denote the year of the last confirmed positive sighting. The only possible states of nature over a T year period are then either $\sigma_i = x$ for all $i = 1, 2, \ldots, T$,

$$\boldsymbol{x} = (x, x, x, \ldots, x),$$

or $\sigma_{j-1} = x$ and $\sigma_j = e$,

$$\boldsymbol{e_j} = (x, x, \ldots, x, e, e, \ldots, e), \quad j = T_N + 1, \ldots, T,$$

and the first e entry in $\boldsymbol{e_j}$ is in the jth position. It is important to note from the above remarks that the state of $\boldsymbol{x}$ is equivalent to the species being extant at time T which we denote by the event X_T, and $\boldsymbol{e_j}$ is equivalent to the species becoming extinct (as opposed to being extinct) in year j which we denote by the event E_j. The problem of interest is to estimate the conditional probability that the species is extant in year T given a sighting record $\boldsymbol{s}$. From the definition of conditional probability this probability can be expressed as

$$P(X_T \mid \boldsymbol{s}) = \frac{P(X_T \text{ and } \boldsymbol{s})}{P(\boldsymbol{s})} = \frac{P(\boldsymbol{s}|X_T)P(X_T)}{P(\boldsymbol{s})}. \tag{1}$$

Similarly we can write

$$P(E_j \mid \boldsymbol{s}) = \frac{P(E_j \text{ and } \boldsymbol{s})}{P(\boldsymbol{s})} = \frac{P(\boldsymbol{s}|E_j)P(E_j)}{P(\boldsymbol{s})}, \tag{2}$$

for $j = T_N + 1, \ldots, T$. The events X_T and E_j, $j = T_N + 1, \ldots, T$ are mutually exclusive and exhaustive. Hence the normalisation constant (when the probabilities (1) and (2) are known, or given as point estimates):

$$P(\boldsymbol{s}) = P(\boldsymbol{s}|X_T)P(X_T) + \sum_{j=T_N+1}^{T} P(\boldsymbol{s}|E_j)P(E_j), \tag{3}$$

follows from the fact that the sum of (1) and (2) over all states X_T and E_j, $j = T_N + 1, \ldots, T$ is unity. Substituting (3) back into (1) and (2) gives Bayes rule in its most general discrete form. Furthermore, we require the probability that the species extinct in year T is

$$\sum_{j=1}^{T} P(E_j) = 1 - P(X_T). \tag{4}$$

In conventional analysis it is usual to assume equal *a priori* probabilities for the $P(X_T)$ and $P(E_j)$. In the absence of expert knowledge, Bayesian analysis typically uses $P(X_T) = 0.5$ and $P(E_j) = P_E = 0.5$. However, this *modus operandi* has been criticised (Efron, 2013). As an alternative, we utilise the fact that T_N and T can be considered as parameters of the model. Therefore, it is reasonable to assume that $P(X_T)$ depends on T and T_N. This is discussed further in online Appendix B, where we use the model parameters T_N and T to derive estimates for $P(X_T)$ and P_E, to be used at the users discretion.

2.2. Independent sighting states

To simplify the discussion we will henceforth assume that the yearly sighting states s_i, $i = 1, 2, \ldots, T$, are independent events. Noting the equivalence of X_T and $\boldsymbol{x}$, we can write (1) as

$$P(\boldsymbol{s}|X_T) = P(\boldsymbol{s}|(x, x, \ldots, x)) = p_1 p_2 \ldots p_T, \tag{5}$$

where

$$p_i = P(s_i|x), \quad i = 1, 2, \ldots, T, \tag{6}$$

are the conditional probabilities of sighting states s_i in year i given that the species is extant x in that year. Similarly from the equivalence of E_j and $\boldsymbol{e_j}$ we can write (2) as

$$P(\boldsymbol{s}|E_j) = P(\boldsymbol{s}|(x, x, \ldots, x, e, e, \ldots, e)) = p_1 p_2 \ldots p_{j-1} q_j q_{j+1} \ldots q_T, \tag{7}$$

where

$$q_j = P(s_j|e), \quad j = T_N+1, \ldots, T \tag{8}$$

is the conditional probability of sighting state s_j in year j given that the species is extinct in that year. Note that q_j allow us to model false positives in which sightings are reported even though the species is extinct in year j. For the case when sightings are always definite and there are no false positives, we have $q_j = P(0|e) = 1$, for $j = T_N+1 \ldots T$.

Substituting (5) and (7) into (3) and (1) gives the probability that a species is extant given the sighting record $\boldsymbol{s}$:

$$P(X_T|\boldsymbol{s}) = \frac{p_1 p_2 \ldots p_T P(X_T)}{p_1 p_2 \ldots p_T P(X_T) + \sum_{j=T_N+1}^{T} p_1 p_2 \ldots p_{j-1} q_j q_{j+1} \ldots q_T P(E_j)}. \tag{9}$$

Notice that the factor $p_1 p_2 \ldots p_{T_N}$ cancels. This means that when the p_i and q_i are given (or known), only the yearly sighting states after the last positive confirmed sighting (in year T_N) are needed to evaluate $P(X_T|\boldsymbol{s})$ from (9). We note however that such a cancellation only occurs if one assumes that the sighting states are independent. When there are correlations the situation becomes much more complicated as for example in the (quenched) spin-glass problem (Binder, 2001).

The p_i and q_i represent the probability of an observation given that the species is extant/extinct. In reality, these probabilities depend on many factors, such as abundance of the species and whether the species is charismatic. Ideally, p_i and q_i would capture these factors. However, estimating the effects of these ambiguous factors is challenging. For simplicity, we assume that the probability of a particular observation (given extinct/extant) over time is constant. (Nonetheless, the p_i and q_i may still vary with i when multiple observation types are considered.) Despite this simplification, the p_i and q_i are not known and could themselves be considered as random variables. In such cases, noting formal similarities between our general formulation (1)–(3) and the statistical mechanics of random systems (Wang et al., 1990; Binder, 2001), we consider two methods for dealing with randomness in the sighting record: quenched and annealed.

For quenched randomness one takes the averages of the resulting ratio (9) with respect to the randomness in the conditional probabilities p_i and q_i. In other words, for a particular realisation of the p_i and q_i, one evaluates (9) to get $P(X_T|\boldsymbol{s})$. This is carried out multiple times, for various p_i and q_i over their given pdfs. The quenched probability is the average of the resulting $P(X_T|\boldsymbol{s})$'s.

In the annealed approach to model randomness, the set of p_i and q_i might be assumed to continually change or fluctuate when sampling the ensemble of different states. (As such, only the *average* of the sum of (1) and (2) will be unity.) To take this into account, for annealed randomness, one averages separately the numerator and denominator in (9) with respect to the randomness in the p_i and q_i. For this reason the annealed approach will differ from the quenched approach. It is important to emphasise that conventional Bayesian analysis of problems with underlying uncertainties or randomness uses an annealed approach. For example, Bayes factors are ratios of averages.

2.3. A simple example

To illustrate the differences between quenched and annealed approaches to the present problem, consider the following simple situation of a single sighting record over $T=2$ years, $\boldsymbol{s} = (1,0)$. There is a positive sighting in the first year $s_1 = 1$, and no sighting in the second year $s_2 = 0$, hence $T_N = 1$. We define $p \equiv P(0|x)$ and $q \equiv P(0|e)$ so that $p_1 = 1-p$, $p_2 = p$ (from (6)) and $q_2 = q$ (from (8)). Then (9) can be written as

$$P(X_T\Big|\boldsymbol{s}) = \frac{(1-p)pP(X_2)}{(1-p)pP(X_2) + (1-p)qP(E_2)}. \tag{10}$$

Assuming definite sightings only (i.e. $q=1$), and that $P(X_2) = 1-P(E_2)$ is given, the quenched average of (10) with respect to randomness in p can be expressed as

$$P_Q(X_T\Big|\boldsymbol{s}) = \left\langle \frac{(1-p)p}{(1-p)p + (1-p)r} \right\rangle = \left\langle \frac{p}{p+r} \right\rangle, \tag{11}$$

where $r = (1-P(X_2))/P(X_2)$. As noted, the common factor $(1-p)$ in the numerator and denominator cancels. Similarly, the annealed average of $P(X_T|\boldsymbol{s})$ is given by

$$P_A(X_T\Big|\boldsymbol{s}) = \frac{\langle (1-p)p \rangle}{\langle (1-p)p \rangle + \langle (1-p) \rangle r} = \left[1 + \frac{r}{B}\right]^{-1}, \tag{12}$$

where

$$B = \frac{\langle (1-p)p \rangle}{\langle 1-p \rangle}, \tag{13}$$

is the Bayes Factor. The averages $\langle \cdot \rangle$ in (11) and (13) can be evaluated exactly when the pdf for p is uniform on the interval (a,b), $[0 \le a \le b \le 1]$. See online Appendix A for details. Further, in the extreme case $a=b$, both P_Q and P_A collapse to the deterministic value

$$P_Q(X_T\Big|\boldsymbol{s}) = P_A(X_T\Big|\boldsymbol{s}) = P_D = \frac{a}{a+r},$$

corresponding to the point estimate $p=a$ for $P(0|x)$. For $b > a$ the P_A, P_Q and P_D estimates will differ. For example, when $a=0.6$ and $b=0.8$ we obtain

$$P_Q \approx 0.411, \quad P_A \approx 0.407, \quad P_D = 0.375 \quad \text{when } P(X_2) = 0.5;$$
$$P_Q \approx 0.676, \quad P_A \approx 0.674, \quad P_D = 0.743 \quad \text{when } P(X_2) = 0.75.$$

This illustrates sensitivity to the choice of $P(X_2)$ and the important point that there is no general numerical ordering of P_Q, P_A and P_D. There can be considerable variation between quenched, annealed and deterministic estimates for $P(X_T|\boldsymbol{s})$. This difference is explored further in later sections.

3. When sightings are definite

3.1. Formulation

Taking the lead from the simple example in Section 2.3 we now consider the independent sighting states model (9). In any given year the species is definitely seen (as a specimen for example) or not seen at all. That is, there are no sightings that are "false positives". In this case we represent the yearly sighting states s_i as

$$s_i = \begin{cases} 1 & \text{if seen,} \\ 0 & \text{if not seen,} \end{cases} \qquad i = 1, 2, \ldots, T.$$

Thus $s_j = 0$ for $j = T_N+1, \ldots, T$ in the case of definite sightings only. By definition, the last positive sighting was in year T_N, and hence $q_j = P(0|e) = 1$ for $j = T_N+1, \ldots, T$. Assuming there is a total of S positive sightings in the record period (which occur in or before year T_N by definition) and $P(E_j) = P_E$ for $j > T_N$, Eq. (9) gives

$$P(X_T\Big|\boldsymbol{s}) = \left[1 + \frac{P_E}{P(X_T)}(1-p)^{-1}(p^{T_N-T} - 1)\right]^{-1}, \tag{14}$$

from $P(0|x) \equiv p$, $P(1|x) = 1-p$. For further details on the derivation of (14) see online Appendix B. For given p, $P(X_T)$ and P_E, Eq. (14) is the deterministic point estimate $P_D(X_T|\boldsymbol{s})$. Averaging (14) with respect to some pdf for p gives the quenched estimate $P_Q(X_T|\boldsymbol{s})$. Averaging the numerator and denominator separately in (9) gives the annealed estimate $P_A(X_T|\boldsymbol{s})$. The different results from these

two approaches, as well as the deterministic approach (14), are shown in Fig. 1(a) for $p \in [0.6, 1]$, and Fig. 1(b) for $p \in [0.6, 0.9]$. In the case of S and T fixed, and T_N increasing, the quenched approach generally gives a lower estimation that the species is extant.

In certain (asymptotic) limiting cases $P_A(X_T|\boldsymbol{s})$ reduces to a Solow equation (Solow, 1993). This provides a useful connection and check on our annealed formulation. In online Appendix C we show that when $S \ll T_N$ and p are uniformly distributed on $[1-\omega, 1]$, $0 \le \omega \le 1$:

$$P_A(X_T|\boldsymbol{s}) \sim \left\{1+\frac{1-\pi}{\pi S}\left[\left(\frac{T}{T_N}\right)^S - 1\right]\right\}^{-1}. \tag{15}$$

where π is the prior probability that the species is extant over the period $(0, T)$. Notice that (15) is independent of ω to leading order. More generally, if $P(X_T) \neq \pi$:

$$P_A(X_T|\boldsymbol{s}) = \left\{1+\frac{P_E T}{P(X_T) S}\left[\left(\frac{T}{T_N}\right)^S - 1\right]\right\}^{-1}. \tag{16}$$

Eq. (15) first appeared in Solow (1993), but with S replaced by $S-1$. This small difference is because the Solow derivation assumes an improper prior distribution for p. If the upper limit on p is not 1, Eqs. (15) and (16) are incorrect.

Eq. (16) is used in both Fig. 1(a) and (b), where S and T are fixed, and T_N increases. Fig. 1(a) indicates that when the extreme $p=1$ (an observation is impossible) is included, the asymptotic annealed (16) is a very good approximation for the annealed case. This is not the case when the spread for p does not include $p=1$, see Fig. 1(b). Furthermore, Fig. 1 shows that the deterministic (14), which is independent of p, and the asymptotic annealed (16), which is independent of ω, are reasonably similar. For both the quenched and annealed approaches, including $p=1$ results in a higher probability that the species is extant.

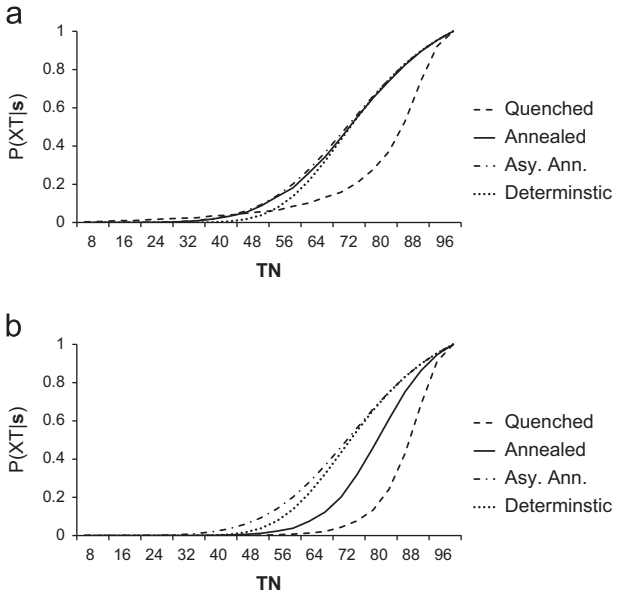

Fig. 1. Definite sightings only $S=5$, and varying T_N such that $10 \le T_N \le T = 100$ ($P(X_T) = T_N/T$, $P_E = 1/T$). The quenched is generated from taking the average of the ratio (9) for $[a \le p \le b]$. Using the same $[a \le p \le b]$, and the same Eq. (9), the annealed is generated from taking the average of the numerator and denominator separately, then taking the ratio. The asymptotic annealed is from (16), and the deterministic is from (14). (a) $0.6 \le p \le 1$. (b) $0.6 \le p \le 0.9$.

3.2. Deterministic estimates

Typically, when expert estimates are unavailable, Bayesian analysis uses an unbiased value of 0.5 for estimates. We use alternative estimates to derive a deterministic estimate $P_D(X_T|\boldsymbol{s})$. We assume that the probability of a definite observation, given that the species is extant, is constant. Given that S positive sightings occurred over a period of T_N years, where it is known that the species is extant, an estimate for p could be

$$p = P(0|x) = 1 - \frac{S}{T_N}. \tag{17}$$

Similar arguments apply to P_E and $P(X_T)$ to give the deterministic estimate

$$P_D(X_T|\boldsymbol{s}) = \left[1+\frac{1}{S}\left(\left[1-\frac{S}{T_N}\right]^{T_N - T} - 1\right)\right]^{-1}, \tag{18}$$

where we have used

$$P(X_T) = \frac{T_N}{T} \quad \text{and} \quad P_E = \frac{1}{T}. \tag{19}$$

Again, calculation details are provided in online Appendix B. It is interesting to note that in the limiting case $S \ll T_N$, Eq. (18) reduces to give $P_D(X_T|\boldsymbol{s}) = P(X_T)$.

3.3. A case study: Caribbean monk seal

The Caribbean monk seal has $S=5$ confirmed positive sightings in years 1915, 1922, 1932, 1948 and 1952, and no further positive sightings in the following 59 years to 2012. The monk seal was thus known to be extant in the 38 years from 1915 to 1952. Hence

$$S = 5, \quad T_N = 38, \quad T = 97. \tag{20}$$

For these values, the deterministic estimate (18) gives

$$P_D(X_T|\boldsymbol{s}) = \left[1+\tfrac{1}{5}\left\{(0.868)^{-59} - 1\right\}\right]^{-1} = 0.0012$$

from $p = 1 - \frac{5}{38} = 0.868$.

Clearly this takes no account of possible randomness in the sighting process itself, including sighting effort. To illustrate the sensitivity of the point estimate (18), assume (20) still holds, but the probability of no sighting given that the species is extant is slightly larger, say $p=0.92$. This changes the probability that the species is extant by an order of magnitude

$$P_D(X_T|\boldsymbol{s}) = 0.0219 \quad \text{from} \quad p = 0.92,$$

where $P_D(X_T|\boldsymbol{s})$ is from (14) with (19). If we take simulated quenched and annealed averages of (9) as described in Section 2.3 we obtain

$$P_Q(X_T|\boldsymbol{s}) = 0.0064 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0065 \quad \text{where} \quad p \in [0.86, 0.92], \tag{21}$$

$$P_Q(X_T|\boldsymbol{s}) = 0.0102 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0179 \quad \text{where} \quad p \in [0, 1], \tag{22}$$

$$P_Q(X_T|\boldsymbol{s}) = 0.0949 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0246 \quad \text{where} \quad p \in [0.86, 1], \tag{23}$$

$$P_Q(X_T|\boldsymbol{s}) = 0.0005 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0034 \quad \text{where} \quad p \in [0, 0.92], \tag{24}$$

for uniform distributions of $p = P(0|x)$ on the stated intervals, $P(X_T) = T_N/T = 0.392$ and $P_E = 1/T = 0.01$. When p lies in a small interval (21), $P_Q \approx P_A$, as expected. Taking p to lie uniformly in the interval (0,1) reflects absolutely no knowledge about the probability of seeing the species, given it is extant (22). In reality, this situation is unlikely. Yet it is interesting to compare the outcomes from

$p \in [0.86, 0.92]$ (21) with $p \in [0,1]$ (22). The latter includes the extremes: a specimen is guaranteed, $p=0$, and it is impossible to detect a specimen, $p=1$. The quenched and annealed estimates diverge as expected, but unexpectedly, including the extreme $p=1$ has a stronger effect than its lower bound counterpart. Including $p=0$ decreases the probability that the species is extant (24), while including $p=1$ increases the probability that the species is extant (23).

Lastly, suppose we do not use T_N and T to estimate $P(X_T)$ and P_E. Instead we take $P(X_T)=0.5$ and $P_E=0.5$, giving

$$P_Q(X_T|\boldsymbol{s}) = 0.0002 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0002 \quad \text{where} \quad p \in [0.86, 0.92]. \tag{25}$$

We observe that P_Q and P_A are influenced by $P(X_T)$ and P_E. Comparing (25) to (21) we note that the former uses a $P(X_T)$ which is only slightly larger, while the P_E is considerably larger. Subsequently (25) presents a lower estimate for the species being extant.

4. Including uncertain sightings

In order to implement our general formulation when there are several independent observational types (specimen, photographs, etc.), it is convenient to represent the various types of sighting records as a matrix of 0's and 1's. Columns correspond to observational types and rows correspond to years. Thus, when we have A types of sighting records labelled $\alpha = 1, 2, \ldots, A$ over a period of T years labelled $i = 1, 2, \ldots, T$, the (i, α) entry of the record matrix, denoted by s_i^α, takes the values

$$s_i^\alpha = \begin{cases} 1 & \text{if seen as a type } \alpha \text{ inyear i,} \\ 0 & \text{if not seen as a type } \alpha \text{ in year i.} \end{cases}$$

Table 1 shows an example of a record matrix with $A=3$, and $T=7$.

When presented as a matrix, it is clear in this example that in year 3 a specimen and sound recording was collected, but there was no photographic evidence. In the following year 4, the year after the last positive sighting ($T_N=3$), there was a photograph, no sound recording, and of course no specimen. And so on for other years. For each $\alpha = 1, 2, \ldots, A$ there are now two independent conditional probabilities, which we express as

$$p^\alpha \equiv P(\alpha, 0|x) \quad \text{and} \quad q^\alpha \equiv P(\alpha, 0|e),$$

corresponding respectively to the species being not seen as a type α observation, given that the species is extant x or extinct e. Note that for definite (specimen) sightings ($\alpha = 1$), $q^1 = 1$.

From the record matrix (e.g. Table 1) we construct the corresponding $T \times A$ conditional probability matrices

$$P = (p_i^\alpha) \quad \text{and} \quad Q = (q_i^\alpha), \tag{26}$$

where

$$p_i^\alpha = \begin{cases} p^\alpha & \text{if } s_i^\alpha = 0, \\ 1-p^\alpha & \text{if } s_i^\alpha = 1, \end{cases} \quad q_i^\alpha = \begin{cases} q^\alpha & \text{if } s_i^\alpha = 0, \\ 1-q^\alpha & \text{if } s_i^\alpha = 1, \end{cases} \tag{27}$$

Table 1
An example of a sighting matrix for three different independent sighting types.

$i \setminus \alpha$	1 (specimen)	2 (photograph)	3 (sound)
1	1	1	0
2	0	0	1
3	1	0	1
4	0	1	0
5	0	0	0
6	0	1	0
7	0	0	1

where $\alpha = 1, 2, \ldots, A$ and $i = 1, 2, \ldots, T$. In our basic formula (9) the p_i and q_i are then simply the products (over $\alpha = 1, 2, \ldots, A$) of the row entries p_i^α and q_i^α for each $i = 1, 2, \ldots, T$ in P and Q (26).

For given p^α, q^α, $P(X_T)$ and P_E, one obtains a deterministic estimate for $P(X_T|\boldsymbol{s})$ directly from (9) using computed values for p_i and q_i as described earlier. If p^α and q^α are taken as random variables with some specified pdf's or ranges of possible values, one repeatedly draws values of p^α and q^α from appropriate distributions to generate values for the p_i and q_i. As described in the previous sections, these are used to estimate the ratio of averages or average of ratios, forming the annealed and quenched estimates for $P(X_T|\boldsymbol{s})$.

In practice, if the p^α are drawn from the same distributions, this implies that the probability of seeing a specimen, photo, etc., given the species is extant, is likely to be the same. However, a sound recording may be more likely than a photograph, which is more likely than a specimen. The p^α distributions should be chosen to reflect this ordering, i.e. $p^3 < p^2 < p^1$ where $\alpha = 1$ is the definite (specimen) record, $\alpha = 2$ is the photograph record and $\alpha = 3$ is the sound recording record. This distinction is more obvious when choosing the distributions for q^α. The probability of a specimen given the species is extant is 0 by definition, hence $q^1 = 1$. Further, a false photograph may be more likely than a false sound recording, meaning $q^2 < q^3 < q^1$. However, usually the rate of false sightings are difficult to estimate, so q^α, $\alpha = 2, 3, \ldots$ may lie within a large range when α is referring to an uncertain sighting record.

In our basic formula (9) the p_i and q_i are simply the products (over $\alpha = 1, 2, \ldots$) of the row entries p_i^α and q_i^α for each $i = 1, 2, \ldots, T$ in P and Q. Table 2 demonstrates this construction for p_i and q_i for the sighting record matrix in Table 1.

As a numerical example, consider the p^α, $\alpha = 1, 2, 3$ uniformly distributed on

$$\begin{aligned} p^1 &= P(1,0|x) \in [0.2, 0.4], & q^1 &= 1, \\ p^2 &= P(2,0|x) \in [0.4, 0.6], & q^2 &= P(2,0|e) \in [0.2, 0.7], \\ p^3 &= P(3,0|x) \in [0.3, 0.6], & q^3 &= P(3,0|e) \in [0.1, 0.5]. \end{aligned} \tag{28}$$

We use these values to construct p_i and q_i (from Table 2), and to take simulated quenched and annealed averages of (9) as described in Section 2.3. Suppose we do not have estimates for $P(X_T)$ and P_E. In this circumstance, Bayesian analysis typically uses $P(X_T)=0.5$ and $P_E=0.5$. This gives

$$P_Q(X_T|\boldsymbol{s}) = 0.0231 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0151. \tag{29}$$

Alternatively, using $P(X_T) = T_N/T = 0.429$ and $P_E = 1/T = 0.143$ gives

$$P_Q(X_T|\boldsymbol{s}) = 0.0631 \quad \text{and} \quad P_A(X_T|\boldsymbol{s}) = 0.0442. \tag{30}$$

The results (29) and (30) demonstrate that the result is affected by the choices for $P(X_T)$ and P_E. Nonetheless, in this example, the difference is not great. Using the midpoint for p^α and q^α in the above intervals (e.g. $p^2 = 0.5$, $q^2 = 0.45$) gives a deterministic probability,

$$P_D(X_T|\boldsymbol{s}) = 0.0373. \tag{31}$$

Table 2
Constructing p_i from the sighting matrix in Table 1. The q_i are constructed using the same process.

$i \setminus \alpha$	1	2	3	p_i^1	p_i^2	p_i^3	p_i
1	1	1	0	$1-p^1$	$1-p^2$	p^3	$(1-p^1)(1-p^2)p^3$
2	0	0	1	p^1	p^2	$1-p^3$	$p^1p^2(1-p^3)$
3	1	0	1	$1-p^1$	p^2	$1-p^3$	$(1-p^1)p^2(1-p^3)$
4	0	1	0	p^1	$1-p^2$	p^3	$p^1(1-p^2)p^3$
5	0	0	0	p^1	p^2	p^3	$p^1p^2p^3$
6	0	1	0	p^1	$1-p^2$	p^3	$p^1(1-p^2)p^3$
7	0	0	1	p^1	p^2	$1-p^3$	$p^1p^2(1-p^3)$

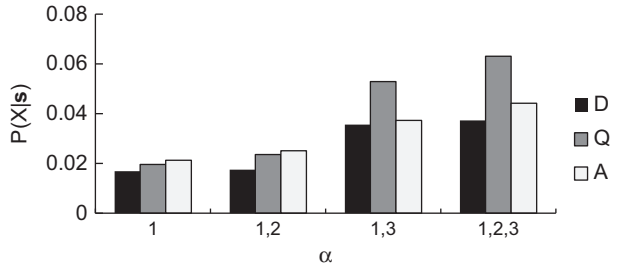

Fig. 2. Results from the example in Table 1 with various combinations of sighting records α, and p given by (28). The deterministic (D) is from (14). The quenched (Q) is generated from taking the average of the ratio (9). Using the same Eq. (9), the annealed (A) is generated from taking the average of the numerator and denominator separately, then taking the ratio.

Notice that $P_D < P_A < P_Q$ (with P_Q and P_A from (30)). Fig. 2 shows how these results compare when uncertain sightings are excluded. Clearly, formally including uncertain sightings can make a difference when estimating whether the species is extinct.

We conclude this simple example by noting that in reality, it may be difficult for an expert to estimate the probability of a sighting given the species is extant $1-p=P(1|x)$ or extinct $1-q=P(1|e)$. Some estimating from given information, such as the probability that a sighting is true, may be necessary.

5. Discussion

We have formulated a method to infer $P(X_T|\boldsymbol{s})$, the probability that a species is extant given the sighting record $\boldsymbol{s}$, as is given by (9). Our formula for this probability is Bayes formula in its most general, discrete form. Calculating $P(X_T|\boldsymbol{s})$ requires estimating the probability of no observation in year i given it is extant, i.e., p_i in (9). We also consider the probability of no observation given that it is extinct, the q_i in (9), to allow for the event of a false sighting occurring after extinction. Obtaining these observation estimates are challenging, and generally experts provide a range for them, or sometimes a pdf. Therefore, an estimate of the final probability $P(X_T|\boldsymbol{s})$ is best taken as an average over the uncertainty (randomness) within the observation probabilities of the p_i and q_i. A simple mean gives the "quenched" average $\langle P(X_T|\boldsymbol{s})\rangle$. Alternatively, the numerator and denominator of (9) may be averaged separately, which is referred to as the annealed approach.

Several other studies (Solow, 1993; Solow et al., 2011; Lee et al., 2013) attempted to estimate $P(X_T|\boldsymbol{s})$ using Bayesian techniques, also taking into account randomness in the observation probabilities. In these works, the expression for $P(X_T|\boldsymbol{s})$ was given in terms of a Bayes factor and is essentially the annealed approach (taking the ratio of averages). Our approach here is far more general than others in the literature but in certain limiting cases, reduces to the results of Solow (1993).

The quenched versus annealed methodologies should be viewed as two competing approaches for studying the effects of randomness. As to which method is the most appropriate, the differences between the approaches are simply the way one prefers to model the randomness of the parameters. The quenched approach assumes that the p_i and q_i are fixed over any simulation of the T years. In contrast, the annealed approach assumes that the probabilities p_i and q_i continually change or fluctuate (according to their pdf's) when sampling the ensemble of different states. There has been a long history of debate in statistical physics as to which is the most appropriate. Neither annealed nor quenched is the 'more correct' approach, but merely two different ways to account for uncertainty in the observation probabilities. In our case, the beauty of the quenched approach is that (because of algebraic cancellations), one needs to only analyse data after the last definite sighting.

We demonstrated the probability that a species is extant depending on the initial estimates of priors $P(X_T)$ and P_E. Generally, uncertainty in the probabilities of observations is of more interest than uncertainty in the priors, since the former is more challenging to define. Nonetheless, assigning a pdf for $P(X_T)$ and P_E estimates is elementary, and could easily be carried out with the same methodology.

We show how our general model can be solved analytically for a number of specific cases. For example, if all sightings are definite, and thus no randomness in the observation probabilities, the model gives an elegant solution (18). Similarly, it is possible to reduce the model for an asymptotic annealed prediction (16), which proves to be a good approximation for the annealed estimate, and under special assumptions reduces to Solow's model (Solow, 1993) to infer extinction.

We considered the Caribbean monk seal sighting data. We first considered $p \in [0.86, 0.92]$, Eq. (21), meaning that an observation (given the species is extant) is unlikely, but possible. It is straightforward to experiment with different choices for the observation probability p, for example see (22) and (23). Under various choices of p we find that the Caribbean monk seal is probably extinct, agreeing with Solow's analysis (Solow, 1993).

Our work agrees with Lee et al. (2013), where it was shown that uncertain sightings can greatly affect the extinction estimation. Furthermore, when a species is thought to be critically endangered, or extinct, surveys are conducted to look for the species. It is straightforward to build upon this method to include survey effort. A versatile numerical format, which has a user-friendly interface, will ensure this work can be used as a decision making tool. This is the subject of forthcoming work, where this method (with an extension to include survey effort) is transcribed to an Excel spreadsheet.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2013.08.023.

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